ASPECTS OF THE ACCUMULATION AND DECOMPOSITION OF WOOD IN THE LITTER LAYER OF A COPPICED BEECH-OAK WOODLAND

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INTRODUCTION

The review by BRAY and GORHAM (1964) suggests that in temperate deciduous woodland about 30 p. 100 of total annual litter fall is in the form of dead wood. In their detailed study of litter production in oak-ash woodland CARLISLE *et al.* (1966) found an annual fall of twigs and branches of 1 164 kg per ha, which was 30 p. 100 of total litter fall. OVINGTON (1961) found that 40 p. 100 of the total energy content of litter fall in a 35 year old *Pinus sylvestris* plantation was contributed by dead branches. The decomposition of leaf litters is a rapid process so that the mineral nutrients that they contain are generally re-cycled within a two-to-four year period. In contrast wood is more resistant to decay and the breakdown period correspondingly longer. Thus although wood is far less rich in mineral nutrients per unit dry weight than leaf material, a significant amount may accumulate in the wood fraction of the litter during the development of mature woodland (OVINGTON, 1959 *a*, *b*). In terms of an energy reservoir the wood fraction of litter is probably even more significant.

In recent years there have been many studies of leaf-litter breakdown and the general features of the process are well known (BURGES, 1967). Although there have been several studies of the communities of organisms associated with rotting wood (CHESTERS, 1950 ; MANGENOT, 1953 ; BUTCHER, 1968 ; LEACH *et al.*, 1937 ; SAVELY, 1939 ; FAGER, 1968) no comparable quantitative studies of wood breakdown in natural situations have been made. This paper is an account of the initial stages of a study of the breakdown of wood in the litter layer of beech-oak woodland at Blean Woods National Nature Reserve, Kent, south-east England. Descriptions are given of methods of sampling and estimating the pattern of distribution, abundance and standing crop of rotting wood, and of identifying the stages of decomposition. More

detailed accounts of the micro-organisms and invertebrates involved in the process of breakdown, and of their contribution to energy flow and nutrient cycling, will be published later.

The experimental site is an area of woodland in which the coppicing cycle has been abandoned for between 40 and 60 years. The trees consist of beech, *Fagus sylvatica* L. (1 303 stools/ha) ; oak, *Quercus petraea* (MATTUSCHKA) LIEBL. (823 stools/ha) and sweet chestnut, *Castanea sativa* MILL. (251 stools/ha). The beech and sweet chestnut trees show the characteristic growth form of abandoned coppice with generally more than one and up to ten stems arising from a common basal stool. One or more stems of a stool are usually dead, particularly in the case of sweet chestnut, but as yet very few of these have fallen. Oak grows mainly as single stems, a high proportion of which are dead, many due to the agency of the wood-rotting basidio-mycete *Armillaria mellea* VAHL. (ex FRIES). The height of the canopy is not more than ten metres. There is no ground flora. The soil is an oligotrophic brown earth on London Clay and has a well developed moder humus form. Most of the wood falling into the litter layer is from lower side branches, although some main stems of oak are also present.

Initially our aims were four-fold : (1) to estimate the abundance of the standing crop of dead wood in the litter layer preparatory to estimating its rate of breakdown ; (2) to investigate its pattern of distribution in the litter layer ; (3) to estimate the proportion of the standing crop at various stages of decay ; (4) to distinguish the major communities of organisms present and involved in the various stages of decay. This paper describes work concerned with the first three of these aims.

SAMPLING

Methods

There are considerable problems in devising a sampling technique for rotting wood. There are at least four sources of heterogeneity in its distribution : (1) it is distributed in the form of discrete units, logs or twigs (unlike leaf litter which is distributed in a relatively even layer) ; (2) these units have very variable dimensions ; (3) the units are not distributed in a random or regular way ; (4) there is variability in the pattern of decay and distribution of organisms in different parts of the logs. In the early stages of this work we developed a sampling technique which we hoped would deal partially with the problem of heterogeneity as well as permitting us simultaneously to work towards the four aims outlined above. The method was based on the techniques of distance sampling (« plotless sampling ») developed by, among others, CLARK and EVANS (1954), COTTAM and CURTIS (1956), COTTAM, CURTIS and CATANA (1957) and KEULS, OVER and DE WIT (1963) and reviewed by GREIG-SMITH (1964) and SOUTHWOOD (1966).

Transect lines, 30 m long, were placed at random in the sampling area and six sampling points, selected from a table of random numbers, located along each of them. At each of these points four right-angled quadrants were defined, two on each side of the line (fig. 1). In each quadrant the distance from the sampling point to the first, second, third, fourth and fifth nearest log was measured. Only logs greater than 2 cm in diameter were included in the sample. Thus at each sampling point the distance to 20 logs was measured. The diameter and length of the fifth nearest log were measured and a sub-sample, 5-10 cm in length, was cut from the region of the log nearest to the sampling point. This sub-sample was used for estimating the state of decay of the log, as described below. The specific identity of the log was also noted where possible. Thus at each sampling point four logs were measured, described and sub-sampled in this way. From the measurements for the four separate quadrants the data for the first to fifth nearest logs to the sampling point could be extracted ; these data are given in Table 1 and illustrated in Figure 1.
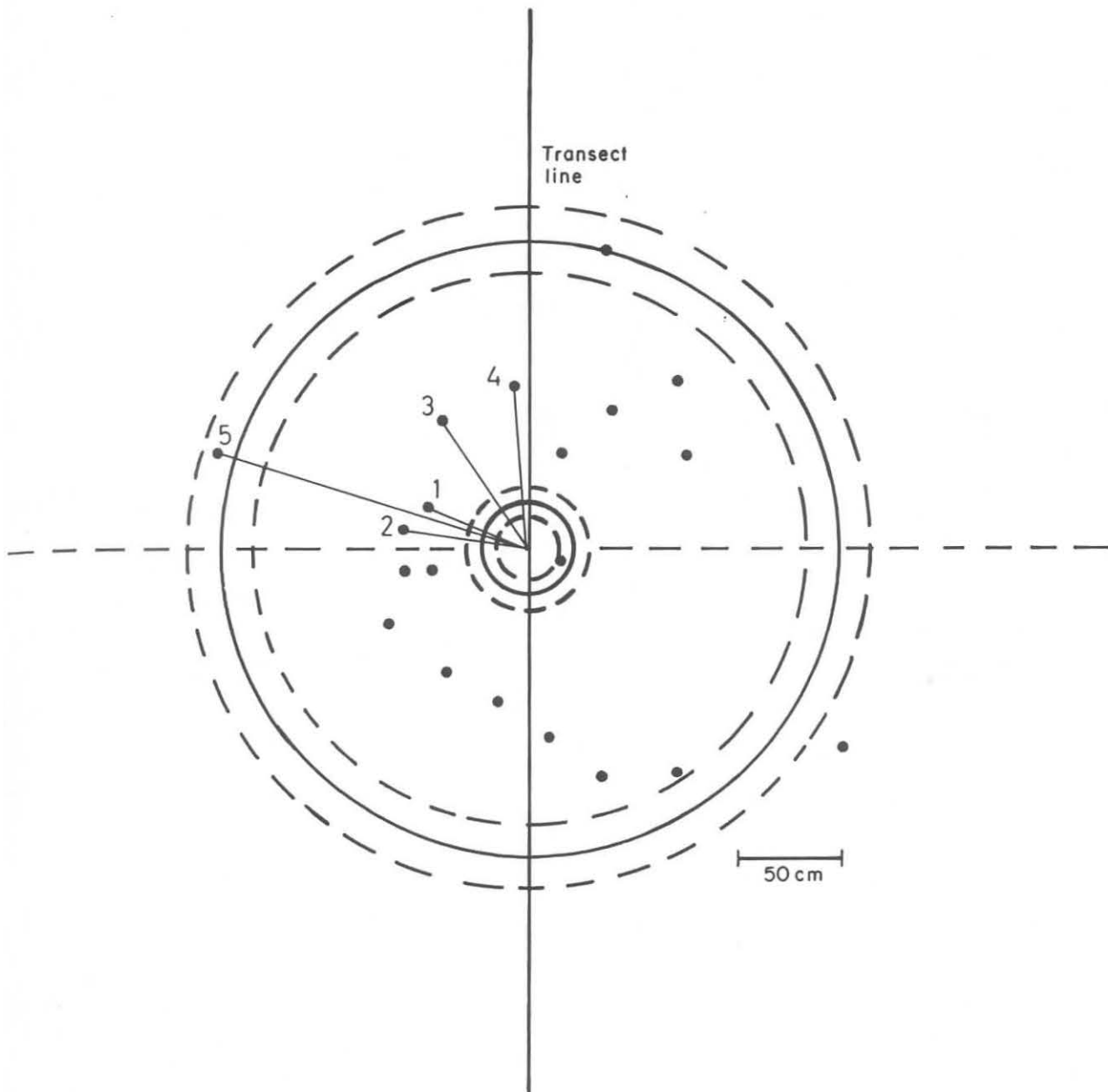
FIG. I. — *A typical distribution of 20 logs around an arbitrarily-selected point on a transect line. The circles drawn in a solid line are mean distances to the nearest and fifth nearest logs, and the circles in dashed lines are their 95 p. 100 confidence limits.*

Results

Most of the methods available for estimating the density of objects from distance sampling data require that the pattern of distribution of the objects is not very different from a random one. Methods that allow for a degree of aggregation in the distribution are in an early stage of development (MORISATA, 1957) and have not been widely tested in field situations. Conversely the methods that permit identification of the pattern of distribution usually require a knowledge of density (PIELOU, 1962). EBERHARDT (1967) has suggested an Index of Non-randomness that is free from this restriction. The index is given by

$$\frac{\overline{(r^2)}}{(\bar{r})^2} = \frac{\text{mean of } r^2}{(\text{mean of } r)^2}$$

where r is the distance from a randomly chosen point to the nearest individual. A random distribution gives an index = 1.27 and values for regular and clumped distributions fall below and above this figure respectively. Unfortunately the sampling distribution of this simple and potentially useful statistic has not been worked out and no test for the significance of deviation from randomness can be made. In the case of our wood data (Table 1), based on a sample of 45 points, the index has a value of 1.656. This is characteristic of a distribution with a fairly high degree of aggregation. On the assumption that it was Negative Binomial in form such a distribution would have a k value a little over 2. This suggests that the distribution of logs in the litter is not random and that methods of density estimation involving that assumption are inapplicable.

The method of KEULS et al., however, is said to be only moderately affected by small departures from randomness. In this method abundance, m, is given by

$$m = \frac{n-1}{\pi} \times \frac{1}{r_n{}^2}$$

where r_n is the average distance from a randomly-selected point to the nearest individual. This method was only doubtfully applicable to our data, but on the basis of the distance to the fifth nearest individual, $(r_5 = 1.48\ m)$ gave an estimated abundance of 0.579 logs per m² with 95 p. 100 confidence limits between 0.287 and 1.327.

TABLE I

Data obtained by distance sampling of logs
Average distance, $\bar{r}$, from 45 random points to the first to fifth nearest logs in m.

$\bar{r}_1$	$\bar{r}_2$	$\bar{r}_3$	$\bar{r}_4$	$\bar{r}_5$
22.5 ± S. E. 3.6	57.4 ± 4.7	88.6 ± 6.2	111.9 ± 7.0	148.0 ± 8.1

| $(\bar{r}_1)^2$ = (mean of r_1)² 1 076.9 | | | $(\bar{r}_1)^2$ = (mean of r_1)² 650.3 | |

Quadrat sampling

Since reliable estimates of abundance could not be obtained from distance sampling, the study was extended to include the analysis of the distribution of logs in 115 quadrats of 1 m². This work was extremely time-consuming and the sample results had high variance. The abundance of logs was estimated as 2.252 ± S. E. 0. 189 per m², with 95 p. 100 confidence limits between 1.893 and 2.611. This is four times the level of abundance estimated by distance sampling, and the two estimates are significantly different. It seems probable that the quadrat sampling estimate is the most reliable and this one is used as the basis of all subsequent calculations. This data provides further evidence that the distribution of logs is non-random, for it gives a value for the Index of Dispersion (DEBAUCHE, 1962) of 192.6 (P < 0.001) and the sample frequency distribution deviates strongly from the Poisson

($\chi^2 = 52.99$, d. f. $= 8$ P < 0.001). If the k parameter of the negative binomial distribution is estimated by the approximate method (SOUTHWOOD, 1966) a value of 3.27 is obtained which (since k is an inverse measure of aggregation) indicates a moderately high degree of clumping. This value is higher than suggested by Eberhardt's Index of Nonrandomness. [It is normal for quadrat sampling data of this type to require logarithmic transformation before analysis, but in this case the variance is not stabilized by transformation, which is frequently found in samples with small means (ANDERSON, 1965)].

THE SIZE DISTRIBUTION OF LOGS

In general the further analysis of the logs was confined to those greater than 2 cm width. A few logs below this size showed evidence of current activity by the wood-boring larvae of *Tipula flavolineata* MEIGEN (a study of which was a subsidiary aim of the work) and these few logs were included in the further analysis. Table 2 shows how the logs were distributed between the taxonomic categories.

TABLE 2

The distribution between taxonomic categories of 127 logs from distance sampling

Beech	Oak	Sweet chestnut	Unidentifiable
81	17	11	18
64 %	13 %	9 %	14 %

Table 3 gives the distribution of the logs in 0.5 cm diameter classes. Nearly half of them (46.5 p. 100) were less than 3 cm in diameter, which emphasises the large number of them which come from small side branches, especially of beech. The distribution of the taxonomic categories between the diameter classes was not signifi-

TABLE 3

The distribution between 10 diameter classes of 127 logs

Diameter (cm) ...	< 2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0
Number of logs ...	5	35	19	23	0
% of sample	3.9	27.6	15.0	18.0	7.1
Diameter (cm) ...	4.0-4.5	4.5-5.0	5.0-5.5	5.5-6.0	> 6.0
Number of logs ..	15	7	10	2	2
% of sample	11.8	5.5	7.9	1.6	1.6

cantly different, although there was a slight tendency for oak and unidentifiable logs to be more frequent in the higher diameter classes. (A much larger sample taken in the quadrat sampling suggests that the original sample may have underes- timated the proportion of small logs ; it may be that as many as 60 p. 100 are below 3.0 cm diameter.)

Logs also vary greatly in length. No lower limit of length was set and we found logs varying from eight to 400 cm long, with the majority (63 p. 100) between 20 and 100 cm. Clearly the best method of analyzing the size distribution of logs is in terms of volume. It was possible to estimate the volume of 123 of the random sample of logs and these had a total volume of 117.7 litres. The distribution of these between nine 0.5 litre volume classes is illustrated in figure 2. In table 4 the data is analyzsed
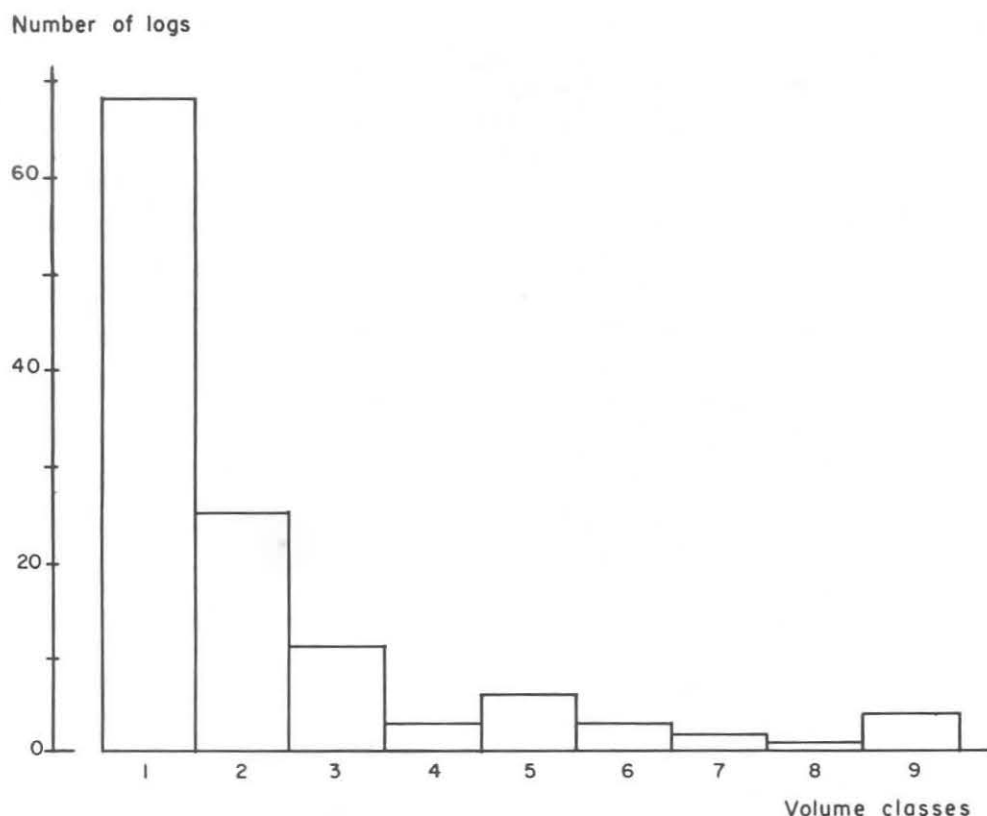

FIG. 2. — *The distribution between volume classes of 113 logs.*
For dimensions of the volume classes see Table 4

in terms of the contribution made by each volume class to the total sample in terms of numbers of logs, in comparison with its contribution to total wood volume. For instance, the smallest class, 0-0.5 litre, contains 55.4 p. 100 (68) of the 123 logs, but these account for only 13.3 p. 100 (15.7 litres) of the total volume of 117.7 litres. In contrast, the largest logs, those over 6 litres in volume, account for only 3.2 p. 100 of the logs but for 24.2 p. 100 of the volume, which emphasises the importance of these few big logs (many of which are main stems of oak) in the total standing crop.

From this data the mean log volume, the average volume of the units of which the standing crop is composed, can be calculated. This is $973 \pm$ S. E. 138 cm^3. From the quadrat sampling data carried out subsequently we have calculated that the

mean volume of rotting wood per m³ is 872 ± S. E. 124 cm³ (95 p. 100 confidence limits 629-1115). No sweet chestnut wood was found in the quadrat sampling ; beech accounted for 74.6 p. 100 of the wood found and oak for the remainder.

TABLE 4

The proportions of 123 logs found in the distance sampling falling into 9 volume classes, and the proportion of the total volume of 117.7 litres in each class

Volume class	1	2	3	4	5	6	7	8	9
Volume range litre	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0	5.0-6.0	> 6.0
Proportion of logs %	55.4	20.4	8.9	2.5	4.8	2.4	1.6	0.8	3.2
Proportion of total volume %	13.3	14.0	10.6	4.3	12.6	8.7	7.8	4.5	24.2

DECAY CHARACTERISTICS OF ROTTING WOOD

Methods

The most direct method of expressing the extent of decomposition of woody material is as a ratio (or percentage) of loss of dry weight against the original. If the original dry weight of the log is not known, or subsampling procedures are adopted, then indirect methods must be used. One such method is to measure change in Relative Density (R. D.), i. e. change in the dry weight per unit volume of wood.
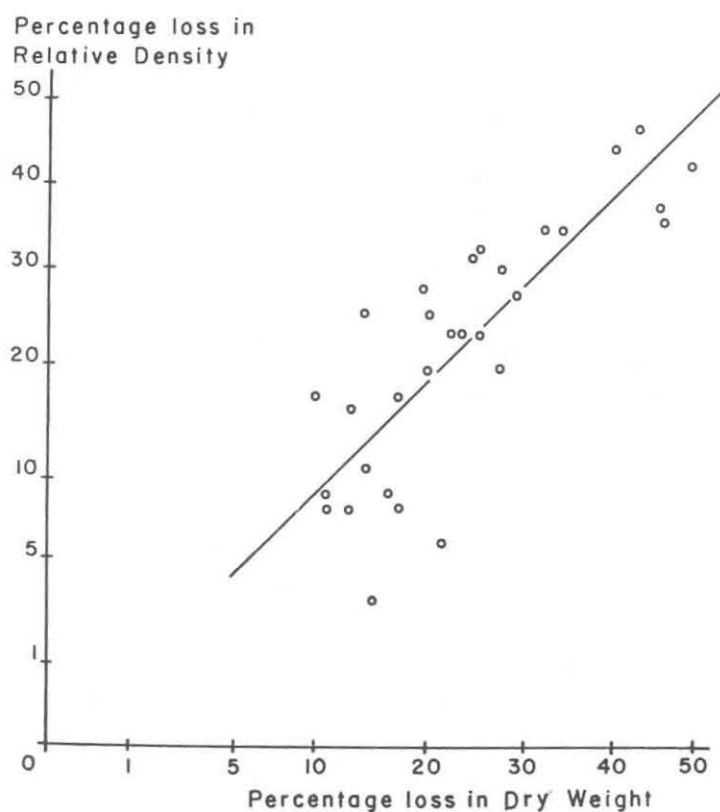

The regression of the percentage loss in relative density on loss of dry weight of 30 beech logs decomposed by Stereum hirsutum. The regression was computed on angular transformed data and the value of the regression coefficient is 1.026 ± S. 0.111 which indicates that the relationship between the two parameters does not differ significantly from 1 : 1.

This procedure was adopted in order to assess the state of decay of logs sampled in the field by the random point selection method. Sub-samples of 5 to 10 cm in length were cut from logs collected in this survey. The length and diameter of the sub-samples was measured to the nearest millimetre, in the field, and the dry weight determined in the laboratory after drying to constant weight at 80°C. From these measurements the R. D. was determined using the formula for a regular cylinder to compute the volume. The chief inaccuracies probably lay in the calculation of the volume, for the samples often deviated from a regular shape. Samples of living wood of beech, oak and sweet chestnut, from a range of different diameter classes, gave coefficients of variation for the R. D. of 6.86 p. 100, 10.41 p. 100 and 10.26 p. 100 respectively.

The potential of R. D. as an estimate of the extent of decay as compared with the direct measurement by dry weight loss is illustrated in Figure 3. Thirty beech logs of known dry weight were inoculated with the wood-rotting basidiomycete *Stereum hirsutum* (WILLD.) FR. and placed in the litter at Blean. Logs were recovered at intervals over a period of twelve months and the R. D. was estimated. The extent of decay of the logs was computed both on the basis of percentage loss in dry weight and as percentage loss in R. D. compared with an original grand mean density for the logs of 0.6400 g/cm³. The regression of R. D. loss on dry weight loss indicates a relationship between the two not significantly different from the theoretical 1 : 1 ratio, thus establishing the utility of R. D. as an estimator of decay.

Results

Figure 4 shows the distribution between twelve relative density classes of 82 logs of beech (59) and oak (23) from the sample collected from the litter and 40 samples of living wood. All the logs were above 2 cm in diameter. Living wood of sweet chestnut had a mean R. D. of 0.500 $\pm$ S. E. 0.012 g/cm³ which was significantly different from those of beech (0.624 $\pm$ S. E. 0.0096 g/cm³) or oak (0.631 $\pm$ S.E
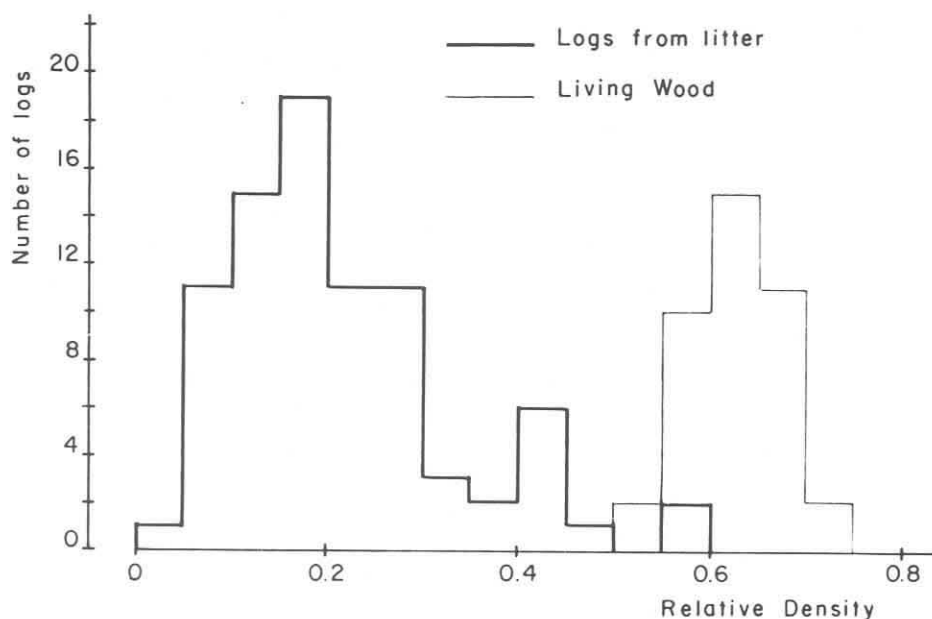

FIG. 4. — *The frequuency distribution of the relative density of 82 dead beech and oak logs and 40 samples of living wood. The class intervals is 0.05 g/cm³.*

0.015 g/cm³) which did not differ significantly. Thus the distribution of R. D. classes of sweet chestnut logs occupied a narrower range than those of oak and beech. For this reason all identified sweet chestnut logs were excluded from the sample.

The frequency and distribution of the R. D. classes showed a wide range, from logs that were very little decayed (0.550 g/cm³) to ones that were almost totally decomposed (0.050 g/cm³). The most interesting feature was the clustering of high

requencies in the lower R. D. classes (mean R. D. = 0.212 $\pm$ S. E. 0.014 g/cm³).
Vhen these densities were compared with that of the grand mean for living beech and
ak logs (0.628 g/cm³) it was clear that over 80 p. 100 of the logs in the litter had
ost more than 50 p. 100 of their original dry weight and 30 p. 100 more than 75 p. 100.

Table 5 shows the distribution of volume of wood per m² for the two main
pecies in terms of R. D. classes. This was compared on the basis of mean wood
olume/m² derived from the quadrat sampling and the frequency percentage of the
ifferent R. D. classes. Also shown is the conversion of these estimates to dry weight
sing the mid-point of the R. D. class as the conversion factor. For total wood volume
he conversion gave an estimate of 185 g dry weight of wood per m² of litter with
95 p. 100 confidence range from 133 to 237 g/m². Of this 78 p. 100 was beech and
2 p. 100 oak.

TABLE 5

Volume and dry weight per m² of oak and beech in different states of decay

R. D. class mid-point (g/cm³)	Oak		Beech	
	Volume (cm³)	Dry weight (g)	Volume (cm³)	Dry weight (g)
0.025	9.6	0.2	0	0
0.075	57.8	4.3	55.2	4.1
0.125	28.8	3.6	132.4	16.5
0.175	38.4	6.7	165.5	29.0
0.225	28.8	6.5	88.3	19.9
0.275	28.8	7.9	88.3	24.3
0.325	9.6	3.1	22.1	7.2
0.375	9.6	3.6	11.0	4.1
0.425	9.6	4.1	55.1	24.4
0.475	0	0	11.0	5.2
0.525	0	0	0	0
0.575	0	0	22.1	12.7
Totals	221.0	40.0	651.0	145.4

DISCUSSION

It is clear that the distance sampling technique cannot at present give adequate
timates of density on populations showing a degree of clumping. The technique
juires considerable development. In this study of rotting wood in the litter layer
technique was valuable in that it provided an excellent method of selecting logs
random, since it required areas to be searched thoroughly so that many small
s hidden beneath the litter were found.

Despite the difficulties of detecting non-randomness in populations of unknown
nsity, the distance sampling technique also provides substantial evidence, later
firmed by quadrat sampling, that the distribution of logs was clumped. Neither
thod permitted us to measure the size or distribution of the clusters in which the

wood is arranged. Rotting wood might be expected on general grounds to be clumped, since the distribution of the trees from which it falls is unlikely to be random. Blean Woods, the site of this study, should probably be regarded as semi-natural woodland. The area has been woodland since at least medieval times, but the present coppice was probably planted in the eighteenth or early nineteenth centuries. Any regularity of distribution has since been lost by outgrowth from stools, activity by pathogenic fungi, windblow, secondary growth etc. so that the prevailing pattern is now an uneven one. Within stools the ages of the stems and therefore the pattern of shedding of dead wood, also varies. Branches tend to break up into a number of separate logs either at time of fall or later, and this process of fragmentation is another factor leading naturally to the formation of clusters of logs. The pattern of the canopy will also influence the distribution of fallen wood.

The clumped distribution of rotting wood has many implications for the biology and dispersion patterns of the organisms that exploit it as a resource. Many of these have further patterns of aggregation within that imposed by the distribution of their substrates and this creates many new sampling problems.

Analysis of the size distribution of logs shows that the majority of them are small, with 55 p. 100 of them less than 0.5 litre in volume and the average log less than 1 litre in volume. Thus the rotting wood substrate is divided into a large number of mostly small units. This is important for the organisms of the rotting wood community which are not able to disperse readily from one log to another if its resources should prove inadequate. The wood-boring tipulid, *Tipula flavolineata*, for instance, may be limited in this way. The adult female lays her eggs in small batches in the bark of a log and typically a number of larvae develop together. They are unable to leave the log until adulthood. Where a group of larvae are occupying a small log they are often much smaller than the rest of their generation and may require a second season to reach pupation (HEALEY, in prep.). Other organisms may be affected similarly, although basidiomycetes are apparently able to produce fruiting bodies when growing in even the smallest logs. On the other hand, the few p. 100 of really big logs present in the litter layer contribute a high proportion of total standing crop volume. These big logs take a long time to decompose and since they present an abundance of energy and nutrient resources combined with the greatest stability and least diurnal and seasonal variability in micro-climate they probably present the most favourable part of the rotting wood standing crop.

The size distribution of rotting wood is likely to be characteristic for any particular woodland. It is likely to be a property of the species of trees present and their age. It does seem probable, however, that in many cases the standing crop may be dominated numerically by small logs. In their study of litter fall in oak woodland, for instance, CARLISLE *et al.* (1966) recorded 64 p. 100 of total wood-fall as « twigs », which they defined as logs below 40 cm long.

Our results suggest that relative density is a reasonably accurate measure of the state of decomposition of wood. Living timber seems to have a remarkably uniform relative density. Beech and oak are not significantly different in R. D. but it is likely that other species, such as sweet chestnut, may be dissimilar. Rotting wood has a much greater range of R. D. than living wood (Fig. 4) and in our experiments on decay of beech logs by *Stereum hirsutum* relative density of the log was an accurate reflection of total loss of material from it (Fig. 3). An interesting feature was the prevalence in

the litter layer of logs with an R. D. averaging around 0.20 g/cm³. This apparent accumulation of more extensively decayed logs has implications with regard to the pattern of decomposition of woody material within the woodland ecosystem. One possible interpretation is that these logs represent a reservoir of the more resistant fractions of the tissues. The low representation of the two lowest relative density classes is probably misleading because at this stage the coherence of the logs is lost and they may be rejected from the survey by the difficulties of sampling and volume measurement. A second possible factor is an extensive period of decay before litter fall ; the activity of wood-rotting hymenomycetes in dead branches on trees is well documented and SHIGO (1967) has described complex communities of fungi and bacteria in such substrates.

From the distribution of relative density amongst the standing crop it is possible to calculate the dry weight of the standing crop. This is an advantage because the direct estimation of standing crop dry weight requires the handling and drying in ovens of a very large volume of wood. R. D. estimation needs only small samples and if the volume of wood in the standing crop has been accurately estimated in the field dry weight can be calculated directly or as in Table 5. Ignoring the small amount of sweet chestnut wood found only in the earliest studies, the 185 g dry weight of dead wood per m² on our site was 78 p. 100 beech and 22 p. 100 oak. It is interesting to note that the standing crop of dead wood in the litter closely reflects the composition of the living stems on the site (Table 6).

TABLE 6

The proportions of living stems and the standing crop of dead wood in the litter that were beech and oak. (A small amount of sweet chestnut is ignored)

	Beech	Oak
Living stems %	71	29
Standing crop of dead wood in litter		
Number %	71	29
Volume %	75	25
Dry weight %	78	22

OVINGTON (1959 b) gives an estimated standing crop of dead wood in the litter layer of a 35-year old *Pinus* plantation of 400 kg/hectare, and this is the only other estimate known to us. Our estimate of 1 850 kg/hectare in a coppiced beech-oak woodland is over four times greater than his. But OVINGTON's site was subjected to management in the removal of lower side branches and thinning of young trees so that comparison with our estimate is difficult. We have as yet no estimates of the rate of fall of dead wood from the trees on our site so that we cannot make estimates of turn-over time for wood tissues. The oak-ash woodland studied by CARLISLE *et al.* (1966) had an annual fall of dead wood of 1 164 kg/ha which is about 63 p. 100 of

our estimated standing crop of dead wood. Unfortunately no real comparison of the work of CARLISLE *et al.* and ours is justified, both because the sites are so different and because it is known that wood fall varies greatly from year to year (BRAY and GORHAM, 1964).

ACKNOWLEDGEMENTS

RÉSUMÉ

ASPECTS DE L'ACCUMULATION ET DE LA DÉCOMPOSITION DU BOIS DANS LA STRATE DE LITIÈRE D'UNE FORÊT DE TAILLIS, DE HÊTRES ET DE CHÊNES

On décrit une étude de l'abondance et de la distribution du bois en décomposition dans la strate de la litière d'un boisement de *Fagus-Quercus*. On a appliqué la technique de l'échantillonnage des distances et celle du quadrat, montrant que les bûches ont une distribution agrégée. On a utilisé la densité relative (g/cm³) pour mesurer la décomposition des bûches et on a trouvé que plus de 80 p. 100 d'entre elles étaient décomposées à plus de 50 p. 100. La plupart des bûches étaient petites, mais les bûches plus grosses contribuèrent en proportion relativement plus élevée au volume total du bois en décomposition. La quantité moyenne de bois en décomposition était de 872 cm³ par m², dont 75 p. 100 de hêtre et 25 p. 100 de chêne, soit 185 g par m², dont 78 p. 100 de hêtre.

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DISCUSSION

G. VANNIER : Les coefficients de transfert de chaleur et de matière sont affectés par la surface extérieure d'un solide (les branches mortes sur le sol pouvant être assimilées à des cylindres) ; pourriez-vous nous donner une idée de la distribution des longueurs des branches tombées qui sont directement liées à leur surface, développées et utilisées dans le calcul des invariants de similitude.

M. J. SWIFT : The distribution of lengths in our log sample was highly variable and it would be difficult to summarize it in any sensible form for a sample as small as 120 logs for decomposition studies. Length may only be an important feature in terms of its relation to what we call the « end-effect ». The exposed ends of logs are important as they are probably the main area of colonization by microbes and animals ; subsamples from the ends of logs have lower RD than central subsamples — a point which must be remembered during field sampling. Short logs tend to have more « end » relative to their total volume than long logs. We have not computed the surface area of our logs but our data will allow this and I am sure it is a feature that is well worth including in our computation.

G. J. F. PUGH : Ascomycetes, and particularly Pyrenomycetes are very important as primary colonizers of branches. Some of them are active parasites and kill the branches (e. g. *Nectria cinnabarina* which is a wound parasite) ; others may be weak parasites which can quickly colonize newly dead branches. Some are confined to the bark, while others can colonize decorticated wood. Some again occur on many types of wood (e. g. *Diatrype stigma*) and some types of wood such as beech have a wide range of fungi on them. Other fungi occur on only one type of wood (e. g. *D. disciformis* on beech) and some trees have only a very limited mycoflora. This is a fascinating group of fungi which deserves further study.

M. J. SWIFT : This paper contains no details of our studies of the biota involved in wood decay. Our approach to this is essentially a functional one *i. e.* to identify the processes of decay and the organisms responsible for them. We shall eventually be able to publish data on the succession of decay organisms from rotting wood. The Ascomycetes will of course receive the attention they deserve within this.

G. MARCUZZI : Points out the importance of water content of logs, since each species of decomposers has a particular optimum of humidity.

I. N. HEALEY : Yes, this is very important. Many factors influence the water content of logs including dimensions (diameter, length), loss or retention of bark, leaf litter cover, growth of mosses or other epiphytes, stage of decay, etc. We are hoping to investigate some of these factors and their influence on organisms.

P. W. MURPHY : Could Dr Swift provide some information on the time taken for the wood

to reach the later stages of decay, *i. e.* when the relative density is about 0.2. I appreciate that this may not be possible at this stage of the investigation. However, it would be very interesting to have an estimate however approximate of the time taken and how much takes place before the woody material reaches the ground.

M. J. Swift : We are unable as yet to give a time scale for the process of decomposition which we have described. What is apparent, however, is that a considerable fraction, one third to one half, of the decay may take place in the canopy prior to litter fall. We have experiments in progress to follow the process through all its stages which should eventually give us the information you seek.

G. Abrahamsen : I wonder if you have measured the ash contents of the logs. Compared with leaves I would assume that the logs are important from a calorific point of view, but from a nutritious point of view they are less important.

M. J. Swift : As you suggest the mineral nutrient content of most woods is low compared with that of leaves. We have not made any estimates on our logs but representative figures can be found in Prof. Ovington's papers.

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